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RUELLIA AND DIANTHERA: AN ANATOMICAL STUDY

THEO. HOLM

(WITH TWO PLATES AND THREE FIGURES)

Many genera of Acanthaceae have been studied from an anatomical point of view, and the literature is quite extensive. Much attention has been given, for instance, to the occurrence of the peculiar cystoliths, which seem to be especially characteristic of this family; the hairs, which are somewhat variable, have been studied also in a number of genera; and the several cases of anomalous stem-structure have attracted much attention. Suggestions as to an anatomical characterization of the family have been made by VESQUE,¹ but only in connection with the leaves. The anatomy of several Ruellieae has been described by OLGA TCHOUPROFF,² and quite a comprehensive anatomical monograph of Thunbergia has been presented by ROULET.³ With the exception of these works, no others dealing with a general treatment of the family have appeared. Therefore, in spite of the rather copious literature, one does not find more than a few scattered notes on the stem structure in general, relatively very little about the leaf, and almost nothing about the roots. It must be remembered, however, that the authors, as a rule, had to depend on herbarium material or specimens cultivated in botanical gardens.

One species of *Ruellia* and one of *Dianthera* are very frequent in the vicinity of Washington, and since these species have not been examined so far, I studied them and found various points that may be of interest to students of plant anatomy. It will be seen from this study that *Ruellia* has a monostelic structure, which is typical of the stem of dicotyledons; while *Dianthera* has a polystelic axis. I was very much surprised in finding such structure in a member of

¹ Caractères des principales familles gamopétales tirés de l'anatomie de la feuille. Ann. Sci. Nat. Bot. VII. 1:326.

² Quelques notes sur l'anatomie systématique des Acanthacées. Bull. Herb. Boissier 3:550. 1895.

³ Recherches sur l'anatomie comparée du genre Thunbergia L. fil. Bull. Herb. Boissier 2:259. 1894.

the Acanthaceae, since it is so very rare among dicotyledonous plants, being known only in *Nymphaea*, *Gunnera*, *Primula* (AURICULA), and *Pinguicula*. In polystelic axes, as described by VAN TIEGHEM and DOULIOT,⁴ each stele has its own pith, parenchymatic rays, mestome, and endodermis, and they are all surrounded by a common cortical parenchyma. When the mestome (leptome and hadrome) is distributed in the axis as several isolated strands, and of mestome alone, such structure is called by the same authors astelic; a structure known in *Anemone*, *Ranunculus*, *Ficaria*, *Caltha*, *Hydrocleis*, etc.

In *Dianthera* the steles are very distinct and readily to be recognized as such, since they are cylindric and possess all the necessary elements. In comparing *Ruellia*, which is a land plant, with the aquatic *Dianthera*, they are found to be very different, and it is interesting to notice in the latter the combination of characters peculiar to aquatic plants in general and others peculiar to Acanthaceae.

Ruellia ciliosa Pursh.

A woodland type from open woods and thickets, associated with *Silphium trifoliatum*, *Salvia lyrata*, *Galactia pilosa*, etc. The stem above ground dies off in the late autumn (November) and the buds that winter over are subterranean. The rhizome, which persists for several years, is creeping and horizontal, or sometimes ascending; the horizontal direction I believe is most typical of the species, and in this the internodes are very short and almost concealed by the numerous thick roots. When the rhizome is ascending, the internodes are more or less stretched and readily visible. The leaves of the rhizome are very short, scale-like, and membranaceous. Several axillary buds are to be observed on the rhizome; in the larger of these, two or three internodes are frequently so distinct that the term shoots might be more correctly applied to these than buds; however, they remain underground during the winter.

The branching of the rhizome is sympodial, and very regularly so, even in old specimens. The apical internode terminates in an aerial shoot, which dies down to the ground at the close of the season, and the continued growth of the rhizome is secured by the develop-

⁴ Sur la polystélie. Ann. Sci. Nat. Bot. VII. 3:275.

ment of an axillary bud. In the accompanying diagram (*diagram 1*), *A* represents the basal portion of the dead stem of 1905; *B*, the aerial shoot of 1906; *L*¹, opposite leaves of the shoot *A*, and in the axil of the one of these (to the right) a small bud (*b*), while in the axil of the other the floral shoot (*C*) is developed. Shoot *C* has also a pair of opposite, scale-like leaves (*L*²), both subtending buds, but of different size, the one behind *C* being the larger (*B*). This large bud (or young shoot) will grow into an aerial stem in 1907, while the two smaller buds (*b*) will remain dormant. The diagram is of a specimen in its fifth year, and not yet blooming.

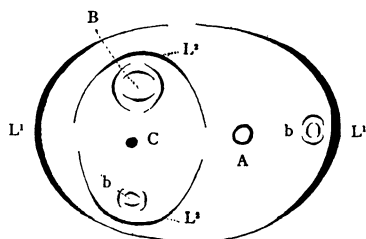


DIAGRAM 1

If we examine the apical portion of a mature specimen with fruits (early in October), the position of the buds is the same as described above, but the number of leaves may be larger. In *diagram 2* the dead stem *A* has one pair of opposite leaves (*L*¹), the one to the right subtending a bud (*b*), while the one to the left subtends a floral shoot (*C*). This floral shoot bears three pairs of leaves with one large (*B*) and three smaller buds (*b*); *B* corresponds with *B* in the diagram described above, and is situated behind *C*. But *B* is here separated from *C* by two pairs of leaves, and thus is situated somewhat lower than in the other specimen, but occupies the same position behind the floral shoot *C*. The large bud in the axil of *L*¹ (to the right of *A*), as stated in the preceding, is so far advanced that the internodes are quite distinct, and this bud sometimes develops into an aerial shoot when *C* becomes injured. Otherwise the rhizome does not branch so as to develop

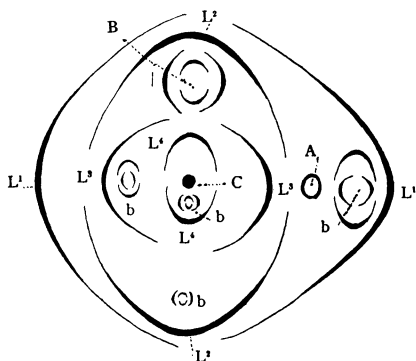


DIAGRAM 2

more than one aerial shoot at the same time; some few specimens I have found, however, where two flowering stems were developed, one of these apical, the other from a bud of a much older portion of the rhizome. Two to five roots develop from the internodes or directly beneath the buds at the nodes.

The rhizome of *Ruellia* is thus relatively short, when it grows in a horizontal direction, and its power to wander is very limited. Nevertheless one may find several specimens with vegetative shoots in connection with a single rhizome and at some distance from it; such cases are not very rare, but these shoots do not arise from the rhizome, but from roots, and are thus simply root-shoots. The diagram of a root-shoot in its first year (*diagram 3*) shows two pairs of scale-like leaves, one central vegetative shoot (*A*), one large bud (*B*) behind this, and another one (*B*) to the right, while a smaller one (*b*) is situated in the axil of L^1 to the left of *A*. The position of the buds is essentially the same as in the other diagrams, with the exception that the aerial shoot (*A*) occupies here the center of the diagram and the apex of the young rhizome, since this is in its first year of growth.

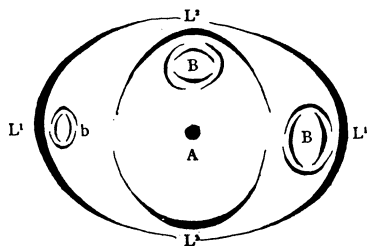


DIAGRAM 3

It is readily seen from these diagrams that in young specimens, in this case a root-shoot, the aerial stem terminates the rhizome in the first year of its growth (*diagram 3*). In older rhizomes, on the other hand, the aerial stem terminates only the apical internode and has actually arisen from the axil of a leaf borne upon the basal internode of the shoot of the preceding year. The shoot *A* is thus always terminal, and always the mother shoot of *C*.

The occurrence of root-shoots has not been recorded for *Acanthaceae*; at least they are not included in WITTROCK's extensive list of "plants with root-shoots."⁵ Three types of such shoots are proposed by WITTROCK: reparative, additional, and necessary; those of

⁵ Om rotskott hos örtartade växter. Förhndlgr. Botan. Sällsk. Stockholm. 1883. [Bot. Notiser 1884:1.]

Ruellia belong to the second type, the additional, which develop spontaneously upon the uninjured plant, and which constitute an important addition to the subterranean vegetative organs. This category of root-shoots is the one that is best known and most frequent; our species of *Apocynum* illustrate this manner of propagation in a striking degree, and I have seen as many as ten flowering stems of *A. cannabinum* developed upon one single root;⁶ it is also the kind so commonly met with in *Sassafras*, *Rhus Toxicodendron*, *Comandra*, etc. It may be stated at the same time that the development of additional root-shoots appears to be characteristic of plants in certain localities; for instance, on the plains of Colorado I noticed a remarkably large percentage of plants of various families that exhibited this peculiar mode of propagation.

THE ROOTS

In mature specimens the secondary roots are quite thick, somewhat fleshy, and of a light brown color. The epidermis is thin-walled and somewhat hairy; it covers an exodermis of one layer, which is also thin-walled and whose cells show the same lumen and shape as those of the epidermis. The cortex is differentiated into three distinct zones: a peripheral of three layers of more or less thick-walled cells with many cystoliths; about nine strata inside the peripheral, which consist of thin-walled cells with rhombic intercellular spaces, and of very thick-walled sclerotic cells (*figs. 1, 2*) besides cystoliths, while no raphids were seen, and no deposits of starch; the innermost stratum, represented by a thin-walled endodermis of small cells and with the Casparyan spots very plainly visible.

The sclerotic cells are very characteristic and readily noticeable by their narrow lumen and porous walls; they are stained bright yellow by chlor-zinc-iodin. Similar sclerotic cells are known also from the roots of *Thunbergia annua*, according to ROULET (p. 343). The cystoliths of the Acanthaceae are very well known, and have been described very carefully by SOLEREDER (p. 697). They vary somewhat in outline, from almost quadrangular to fusiform with the

⁶ That the horizontal shoot-bearing roots of *Apocynum* have been mistaken for "horizontal rootstocks" may be seen in MILLER: Dogbanes of District of Columbia, Proc. Biol. Soc. Washington 13:79.

ends obtuse or acute; their surface, however, is always very distinctly granular. Viewed in longitudinal sections the cells containing cystoliths are usually shorter than the sclerotic. The cortical parenchyma of *Ruellia* thus shows a very characteristic structure.⁷

Inside the endodermis is a thin-walled, continuous pericambium, which surrounds the mestome with its mechanical support of stereome. There are four strands of stereome, each consisting of five to twelve typical stereome cells in one or two layers between the pericambium and the leptome. The leptome itself shows the presence of raphidines, but they seem to be very scarce in this species of *Ruellia*, since I never found more than one in each cell, and only in a very few places. Raphidines were first described by RUSSOW,⁸ who observed them in the root, stem, and leaf of *Hexacentris coccinea*, etc. VESQUE⁹ has also described them as characteristic of *Cyrtanthera*, *Meninia*, *Adhatoda*, and *Fittonia*; while ROULET (*l. c.*) found them in a number of species of *Thunbergia*. They are also to be observed in *Mendoncia* and *Pseudocalyx*, according to RADLKOFER.

The hadrome contains numerous vessels which extend to the center of the root, but secondary formations had already commenced so that the primitive organization of the stele could not be ascertained; however, the four strands of stereome may indicate a tetrarchic structure. Although the specimens of *Ruellia* were collected as late as the third week of September, no deposits of starch were observed in the roots.

Besides the thick, somewhat fleshy secondary roots, there are some that are quite thin on account of the less development of cortex, which consists only of three strata, thin-walled throughout, with no

⁷ A cortex of exactly the same structure has been described and figured by HENRY G. GREENISH (Pharm. Jour. and Trans. London 1891:839) as representing that of the root of what he took to be *Phlox carolina*. However, the root of that species does not possess cystoliths or sclerotic cells, nor do the roots of any other species of *Phlox* that I have examined. The rhizomes and roots which GREENISH had before him, and which were sold as those of *Spigelia marilandica*, no doubt belonged to our *Ruellia*, a plant that has about the same distribution as *Spigelia*, and whose rhizomes somewhat resemble those of *Spigelia*. Hence the statement that cystoliths occur in the root of *Phlox carolina* (SOLEREDER, p. 622) may be safely omitted.

⁸ Sitzungsber. Naturf.-Gesells. Dorpat 5:308. 1878-1880.

⁹ Sur quelques formations cellulosiennes locales. Ann. Sci. Nat. Bot. VI. 11: 181.

sclerotic cells, but with a few cystoliths. The stele is composed of three rays of hadrome, and no secondary growth was yet observable.

The capillary, lateral roots are more hairy than the mother root; they have an exodermis whose cells are larger than those of the epidermis and of the peripheral stratum of cortex. The cortical parenchyma is very thin-walled and contains neither cystoliths nor sclerotic cells; the stele shows two rays of vessels with thin-walled conjunctive tissue; but no stereids and no raphidines were observed in these very thin roots.

The roots of the Acanthaceae have been studied only from a relatively small number of genera, and it seems very likely that the structure described above may be observed in several other species of *Ruellia* and in many other genera of the family, as already indicated in the works of RADLKOFFER, ROULET, RUSSOW, and VESQUE.

THE RHIZOME

As stated above, internodes of the rhizome are either very short and horizontal, or stretched and ascending. The latter form shows the following structure: the epidermis is perfectly glabrous and smooth, with the outer cell walls thickened, and some of the cells containing cystoliths; three continuous layers of collenchyma with cystoliths surround the cortex, which consists of five strata, whose thin-walled cells increase in size toward endodermis and contain many cystoliths and raphids, but only a very few sclerotic cells, and no starch; the endodermis is thin-walled and the cells are much smaller than those of the adjoining cortical parenchyma; a few stereids are located inside the endodermis; and the stele shows an almost confluent zone of leptome and numerous rays of vessels (about ten in each row) with narrow parenchymatic rays; a broad, thin-walled pith occupies the central portion of the stele, in which cystoliths and deposits of starch were observed. A longitudinal section of the internode shows the raphid cells to be very narrow, but much longer than the cells of the cortex proper; the cystoliths vary in length, those of the collenchyma being longer than those of the cortical parenchyma, and obtuse or attenuate at each end.

THE STEM ABOVE GROUND

The basal internodes are obtusely quadrangular and hairy with glandular or pointed hairs of the same structure as those of the leaves (*figs. 3, 4*). The cuticle is smooth, and the cells of epidermis are small, somewhat thickened on the outer wall, and contain cystoliths. Five layers of thick-walled collenchyma surround the cortex, which is thin-walled and consists of about nine strata with wide rhombic intercellular spaces; cystoliths and raphids occur in the cortex, but no sclerotic cells and no deposits of starch. A thin-walled endodermis surrounds the stele, which is obtusely quadrangular in cross-section. A few scattered stereomatic cells are located inside the endodermis and outside the leptome. The mestome strands are collateral; the hadrome is represented by short rays of vessels, separated by mostly four rows of thick-walled parenchyma; a few layers of cambium are observable between the leptome and hadrome, but none outside the medullary rays. The central portion of the stele is occupied by a thin-walled pith of large cells, several of which contain raphids and crystals of various forms, prismatic, rhombic, etc., but no cystoliths and no starch.

The structure of the apical internodes differs in a few points from that of the basal portion of the stem. For instance, the collenchyma occurs as separate strands interrupted by the cortex, which is rich in chlorophyll but contains no cystoliths. Moreover, the stereome is better developed in the superior internodes, forming an almost closed sheath inside the endodermis, but outside the collateral mestome bundles.

In the nodes there is a much stronger development of the collenchyma than in the internodes, and the cortex does not break through this tissue so as to reach the epidermis. By comparing the structure of a node with that of the internode below, the following deviations were noticed: there are ten continuous layers of collenchyma in the node, but only five and not continuous in the internode; there are seven layers of cortex in the node, but only five in the internode. The stereome inside the endodermis is reduced to a very few cells in the node, while it is much better represented in the internode. The pith occupies a larger portion of the section in the node than in the internodes. Finally, the cells of the cortex and pith show a wider

lumen in the node than in the internode. The nodes of other genera of the same family have been described by RÜTZOU,¹⁰ who found raphidines in the leptome of *Schaueria* and *Beloperone*.

THE LEAF

The ample blade is hairy on both faces, especially on the lower, and along the margins; the ventral face is very smooth, while the dorsal shows a prominent keel from the midrib, and also some of the secondaries (the basal) project on this face. The structure is bifacial in respect to the distribution of stomata and the differentiation of the chlorenchyma.

A very simple and uniform structure is to be observed in the cuticle, which is quite thin and smooth on all parts of the blade; and with the exception of the occurrence of the stomata only on the lower face, the structure of the epidermis is identical on both faces. The lateral cell walls are prominently undulate (*fig. 3*) in the ordinary epidermal cells, or straight in those that contain cystoliths (*fig. 3*). Viewed *en face*, the cells containing cystoliths are readily distinguished by their long and narrow outline and by their contents; they abound especially on the dorsal face, underneath the collenchyma, but they are also very frequent between the veins, above and below the chlorenchyma. Glandular hairs with round pluricellular heads are scattered on both faces, but not so frequent as the very long pointed ones (*fig. 4*). The stomata have two subsidiary cells vertical on the stoma, a structure that is also characteristic of certain genera of Caryophyllaceae. Viewed in transverse sections, the cells of the epidermis are quite large, especially above the palisade tissue; but a considerable decrease in lumen is noticeable in that part of the epidermis that covers the collenchyma, that is above and below the larger veins, where the outer cell wall also becomes moderately thickened. The stomata are raised a little above the adjoining epidermis, and the air-chamber is deep and wide.

The mechanical tissue is represented only by hypodermal strands of a few layers of thick-walled collenchyma, which follow the stronger veins, especially the midrib. No stereome was observed. A thin-walled water-storage tissue occupies the greater portion of the promi-

¹⁰ Om Axeknuder. Bot. Tidsskr. Kjøbenhavn. 1880-1: 257.

nent midrib, above and below the mestome bundles. This tissue is also represented, though less developed, on the leptome side of the secondary veins, but only the stronger ones that proceed from the base of the midrib.

In proportion to the size of the leaf-blade, the chlorenchyma is very thin and consists of one layer of typical palisades on the ventral face, and of an open pneumatic tissue on the dorsal; the latter is composed of two to three strata of oblong or more or less roundish cells with very wide intercellular spaces. The chlorenchyma is partly interrupted by the collenchyma above the midrib, but the palisades extend for some distance through the water-storage tissue above the mestome bundles of the midrib (*fig. 6*). According to VESQUE (*l. c.*, p. 333), the palisade tissue is continuous, that is, not interrupted by collenchyma, in *Ruellia maculata* and *R. formosa*, in various species of *Eranthemum*, *Strobilanthes*, *Beloperone*, etc., but interrupted, as described above, in *Sanchezia*, *Ebermayera*, etc.

All the mestome bundles are collateral; those that constitute the midrib are arranged in a broad arch with the concave face turning upward; the others follow the chlorenchyma in one plane. Only the smallest ones, which are not accompanied by water-storage tissue, have a closed colorless and thin-walled parenchyma sheath. The midrib is composed of several (mostly five) mestome strands, separated from each other by strata pertaining to the water-storage tissue; the hadrome consists of a few rows of rather narrow vessels, with three to four in each row. The leptome (*fig. 5*) is well-represented as several groups underneath the hadrome, and also occurs as small, isolated strands between the hadromatic rays (*L* in *fig. 5*). No closed parenchyma sheath is observable in the midrib, but there is nevertheless an endodermis. This very characteristic sheath is represented here on the leptome side only; it is thin-walled, like the adjoining water-storage tissue, and shows very plainly the spots named after Caspary. Without forming a closed sheath, the endodermis thus forms an arch parallel with the keel, and ceases outside the leptome of the two outermost mestome strands. A like structure in regard to the open endodermis in the midrib is described by ROULET (*l. c.*) as characteristic of certain species of *Thunbergia*, for instance, *T. fragrans*, *T. hastata*, and *T. hirta*.

The portion of the blade described above was near the middle, where the leaf is broadest; however, the structure is essentially the same throughout. At the narrow apex there is only a decrease in width of the collenchyma, the water-storage tissue, and the midrib, which consists only of three almost confluent mestome strands; while the chlorenchyma has not undergone any change.

Characteristic of the leaf of our *Ruellia*, therefore, is the interruption of the chlorenchyma by the collenchyma, and the presence of isolated leptomatic strands between the rays of hadrome. The structure of the stomata, the presence of glandular and long pointed hairs, and the cystoliths are, so far as we know, characteristic of *Acanthaceae* in general.

THE PETIOLE

A transverse section of the very short petiole shows an approximately crescent-shaped outline, the ventral face being almost flat in contrast with the dorsal, which is obtusely carinate. The structure is almost identical with that of the midrib in the blade. Glandular and pluricellular pointed hairs occur also, and two or three strata of thick-walled collenchyma follow the outline inside the epidermis. A colorless, thin-walled water-storage tissue occupies the greater portion of the section, and the mestome bundles are arranged in an arch as in the midrib, while two very small strands of mestome are located in the thin margins, surrounded by chlorophyll-bearing parenchyma.

Cystoliths are abundant in the epidermis, but are absent from the colorless parenchyma, in which only raphids and some long prismatic crystals were noticed. On one side of the broad arch-shaped midrib two wide sclerotic cells were observed, and a few raphidines in the leptome.

Dianthera americana L.

This species is very frequent in the vicinity of Washington, D. C., where it grows in creeks and in the Potomac River, generally associated with *Saururus*, *Sagittaria*, *Pontederia cordata*, etc. It has a very long, horizontally creeping rhizome, with opposite, scale-like leaves and stretched internodes of an obtusely hexagonal outline. Secondary roots, from four to eight or even more, are developed at

the nodes, but not directly underneath the leaves, mostly between them; the roots are quite thick and long, and branch freely. The rhizome represents a sympodium, being terminated by a floral shoot, which dies off at the end of the first season; axillary buds occur on the rhizome and at the base of the aerial shoot, and these winter over and continue the growth of the rhizome at the beginning of the next season.

The germination seems to be unknown, and I regret to say that I have never succeeded in studying the young stages of this common plant.

THE ROOTS

As described above, the rhizome is amply provided with roots (secondary), that are quite thick and much branched; they remain active for at least two years and represent a combination of storage and nutritive roots, but are not contractile. The internal structure of these secondary roots exhibits very plainly the features characteristic of roots of aquatic plants. The epidermis is very small-celled and glabrous. The exodermis consists of three very distinct strata (*fig. 8*) of polygonal cells with the walls slightly thickened and deep brown, but with no foldings. The cortical parenchyma is thin-walled and consists of about seventeen layers, the cells very regularly radially arranged and traversed by wide lacunes from the radial collapsing of several of the strata; the outermost layer of the cortex and the innermost three usually remain intact. Small quantities of starch, but no crystals, were observed in the cortex. The stele shows a thin-walled endodermis and pericambium, which was never found to be interrupted by the proto-hadrome vessels. Although these roots have increased in thickness, the primitive organization is yet quite distinct, there being mostly five rays of hadrome with old vessels. The cambial arches inside the leptome (*fig. 7*) are readily visible, as well as the very thin-walled young vessels. The leptome is well represented, and in several cases it appeared as if there were two proto-leptome cells in each strand. A thin-walled conjunctive tissue occupies the inner portion of the stele like a central pith.

No crystals were observed in any parts of these roots, nor any sclerotic or stereomatic cells; in the leptome, however, a few raphidines were noticed, but only in some of the roots. By studying the

same root at different places, I noticed that the collapsing of the cortex does not take place in the entire length of the root, but only in the basal (thickest) portion. The occurrence of raphidines is very variable; in some roots they were observed only in the younger apical portion; in others they were found also in the basal.

The lateral roots of the first order show the same structure as the mother root, but the number of strata in exodermis and cortex is generally smaller. The exodermis, for instance, may be represented by only a single layer, but sometimes three are found, as in the mother root. The cortex may be solid or collapsed, and may be reduced to only three strata. The epidermis does not differ from that of the secondary root, and is glabrous. The endodermis is thin-walled, and the secondary formations are usually not so advanced but that the primitive organization may be readily observed to be diarchic or tetrarchic.

A corresponding structure is to be found in the lateral roots of the second order. They are capillary and have a glabrous epidermis and an exodermis of two layers. The cortex consists of three thin-walled strata, which are collapsed at the base of the root, but entire near the apex. Inside the continuous pericambium are a few stereomatic cells, mostly only two, diametrically opposite each other. The leptome is represented by two broad strands alternating with two rays of hadrome with two wide reticulate vessels in the center, and about three scalariform outside. No secondary growth takes place in these roots.

If it were not for the presence of raphidines, the root of *Dianthera* would be utterly unlike that of *Ruellia* described above. Moreover, the habitat of *Dianthera* is naturally the cause of the very different development of exodermis and cortex, and of the absence of cystoliths, sclerotic cells, and crystals.

THE STEM

The rhizome with the stolons and the ascending aerial shoots show the same structure in general, and, as stated above, the axis is polystelic.¹¹ This peculiar structure was observed in all the inter-

¹¹ A polystelic stem is also possessed by *Dianthera crassifolia* Chapm. and *D lanceolata* (Chapm.) Small, but not by the following species: *D. comata* L. (Porto

nodes of the rhizome and of the ascending shoots, in the slender as well as in the more or less swollen portions of the vegetative axis. In the nodes the polystelic structure becomes somewhat obscured by the anastomoses of the steles; nevertheless, the presence of several steles is usually recognizable.

In outline the rhizome is obtusely hexagonal and smooth; no stomata, but small, sessile glandular hairs were observed. Formations of cork develop from the epidermis, including the cells with cystoliths (*fig. 16*). Inside the epidermis there is a continuous zone of very thick-walled collenchyma of about six layers, bordering on the cortical parenchyma. The cortex consists of numerous strata of thin-walled cells, which are round in transverse sections and with relatively wide intercellular spaces (*fig. 17*); starch was observed in the cortex, and numerous bundles of true raphids, but no chlorophyll. Throughout the internodes of the rhizome (and also of the aerial shoots) the cortical parenchyma represents a homogeneous tissue from the periphery to the central portion, whether a central stele is present or not. No central pith is differentiated in the internodes except where there is a central stele, also a small tissue of this parenchyma is to be found in the peripheral steles. It appears as if the horizontal internodes of the rhizome have always six peripheral and one central stele; these steles are cylindrical and each is surrounded by a thin-walled endodermis with the Casparyan spots plainly visible and with deposits of starch. Inside the endodermis are a few cells of thick-walled stereome, but too few to form a sheath. In the peripheral steles the leptome and hadrome form an almost complete ring, with a small central pith; in the central stele, on the other hand, the mestome is arranged in two arches, with a broad parenchyma in the middle.

Between the leptome and hadrome are a few strata of cambium, and between the strands of mestome are three or four rays of thick-walled parenchyma. Raphidines (*fig. 18*) were observed very frequently in the leptome.

Rico), *D. glabra* B. et H. (Costa Rica), *D. incerta* Brandg. (Lower Calif.), *D. ovata* Walt. (Florida), *D. parvifolia* B. et H. (Texas), *D. pectoralis* Murr. (St. Croix), and *D. sessilis* Gray (St. Domingo). Of these nine species I had only dried material, which was quite sufficient for a study of the steles, but not of the anatomical structure in general.

In a stolon, terminated by an over-wintering bud, I found the same structure as described above as characteristic of the main rhizome, the only difference being that the collenchyma was less thick-walled; that the cortex contained large deposits of starch; and that the central stele showed very prominently three arches of mestome (leptome, cambium, and hadrome) separated from each other by very broad rays of thin-walled parenchyma. While the hadrome in this stele was thus confined to three arches of collateral mestome strands, the leptome was developed as isolated groups inside the endodermis, not only outside the hadromatic rays, but also between them.

While thus the peripheral steles of the main rhizome and the stolons show an almost equal development of collateral mestome strands around a central pith, the stele in the center shows the hadrome more or less distinctly combined in arches (two or three), while the leptome follows the entire periphery inside the endodermis (*fig. 14*).

A corresponding structure is to be found in the aerial shoot which bears the long, narrow leaves and the inflorescences. In the apical internodes, for instance, we find the same tissues and arranged in the same manner, but the change of medium naturally brings about certain modifications of structure. In the rhizome and in the submerged portion of the ascending shoots the cortex does not reach the epidermis, but is completely inclosed by the collenchyma. In the aerial internodes, on the other hand, the cortex extends to the epidermis, thus breaking through the collenchyma, which here becomes developed as isolated strands, as prominent ridges; where the cortex reaches the epidermis it develops typical palisades, which contain much chlorophyll (*fig. 21, C*).

The cuticle is very smooth and thin in the aerial internodes. The epidermis has stomata and glandular hairs, and contains cystoliths. The collenchyma is very thick-walled and forms eight prominent strands of about ten layers; six of these strands correspond with the six peripheral steles, while the remaining two, which are somewhat smaller than the others, are diametrically opposite each other and between two steles. The cortex is differentiated into one or two strata of palisades, located in the furrows between the collenchymatic ridges; the inner portion of the cortex contains less chlorophyll

and the cells are more roundish in cross-sections; while the innermost, which occupies the greater portion of the internode, is a very open tissue with no chlorophyll, but with some small deposits of starch. The intercellular spaces are quite wide and the general structure of the cortex agrees with that of an aquatic plant. Six peripheral steles are located inside the six collenchymatic strands, while a seventh occupies the center of the internode. They are all orbicular in transverse sections and each has a thin-walled, completely closed endodermis, inside of which is another sheath of about two layers of thin-walled stereomatic tissue. The mestome bundles of the peripheral steles are collateral and arranged in an arch toward the periphery of the stem, while the inner face of the steles is occupied by a pith and a few scattered strands of pure leptome (*fig. 14, L*). The central stele shows the same structure as the peripheral. *Fig. 13* shows the mestome of one of the peripheral steles; there are a few strata of cambium inside the leptome, and some young (three) vessels besides older ones in two rays with thin-walled parenchyma between. The node above this internode shows at once a change in the disposition of the steles, that is, four of the peripheral have fused together in pairs so as to form two large steles of triangular outline, while the central and the remaining two peripheral are unchanged. The steles that thus fuse together in the node are those of the internode which are marked *S* in *fig. 9*, and between which there is an isolated strand of collenchyma.

In this node the thin-walled collenchyma surrounds the cortex completely, which is here almost destitute of chlorophyll and which represents a more compact tissue than in the internode below. No raphidines were observed in the node, but many crystals of various kinds, needle-shaped, rhombic, prismatic, etc., abound in the pith of the broader steles.

A dilation of some of the steles thus takes place in the node, resulting in the gradual conrescence of two steles on each side of the node. From the union of these steles each of the two opposite leaves receives three mestome cylinders, readily observed in the petiole as one central, very broad, and arch-shaped cylinder, with a much smaller one on either side. By following the structure of several internodes of a single shoot, I noticed that the central stele is not

present in all of them. Sometimes this central stele was observed in every other internode, but I found also some cases where the apical and basal internodes possessed such a central stele, but not the two internodes between them.

In the basal internodes of the aerial shoots the structure of the stele becomes more regularly developed, the leptome and hadrome forming an equally broad ring around the central pith, which consequently becomes much reduced in width; in other words, these steles show exactly the same concentric and uniform structure as the central stele of the monostelic axes.

In very small vegetative shoots, developed in the axils of the leaves of the larger floral ones, the structure is as described above, but the number of steles may vary. For instance, in a shoot consisting only of two short internodes, the basal one contained only four steles, all peripheral, while the upper one had one central, two large peripheral, and two still broader ones, each of which consisted of two that had partly fused together; the latter corresponding in position with the four marked *S* in *fig. 9*. In these internodes the structure and disposition of the collenchyma and cortex was exactly as described above.

In order to ascertain the number of steles in the stem of *Dianthera*, I examined shoots of very different height and thickness, but the number never exceeded seven—six peripheral and one central. A very thick branch with two opposite and equally robust shoots showed seven steles above and below the node, and also in the two lateral shoots. It is somewhat surprising to see that this polystelic structure ceases at once when the axillary shoot is an inflorescence and not a vegetative branch. The short inflorescence of *Dianthera americana* is borne upon a long, naked internode, and this internode is monostelic from base to apex. In this the cortex incloses completely one broad central cylinder with one zone of leptome and one of hadrome, with parenchymatic rays of equal size and with a central cylindric pith, as is characteristic of monostelic axes.

In the genus *Primula* the Danish botanist VAUPELL¹² detected the polystelic structure in *P. Auricula*, and VAN TIEGHEM and DOULIOT

¹² Om Rhizomets Bygning hos *Primula auricula* og *chinensis*. Vidensk. Medd. Naturhist. For. Kjöbenhavn 1849:76; and Untersuchungen über das peripherische Wachsthum der Gefässbündel der dicotyledonen Rhizome. Leipzig. 1855.

(l. c.) have extended his observation to a large number of species of various sections of the genus. One of the results of their investigation is that a complete accordance exists between the external and internal structure of these species of *Primula*. These authors proposed the reestablishment of *TOURNEFORT*'s genera *Primula* and *Auricula*, the former characterized by possessing a monostelic, the latter a polystelic, axis. Whether this same peculiarity in the stem structure, which I have found in *Dianthera americana*, *D. crassifolia*, and *D. lanceolata*, may be used in classifying the species under two distinct genera, I must leave to future investigators to decide, who have access to more abundant material.

THE LEAF

The narrowly lanceolate and almost sessile leaves are held in a vertical position above the water; they are smooth and glabrous on both faces, while along the margins unicellular, short, pointed hairs occur; over these hairs the cuticle is granulous, but smooth and thin above the epidermis of both faces of the blade. There are only a very few of these hairs, and they were observed only on young leaves.

The leaf is neither exactly dorsiventral nor unilateral, when the distribution of stomata and the structure of the chlorenchyma are considered; the stomata are just as frequent on the ventral as on the dorsal face, and some palisade cells occur here and there inside the dorsal epidermis. Viewed *en face* the cuticle shows no striations, and the lateral cell walls of the epidermis are somewhat undulate on the dorsal face, but almost straight on the ventral; small glandular hairs (*fig. 10*) occur on both faces of the blade. The stomata are not arranged in any way so as to be parallel with the longitudinal axis of the leaf; and they have two subsidiary cells vertical on the stoma. *Fig. 12* shows the commonest form of the outline of the subsidiary cells, which seems to be less regular and more variable on the upper face of the leaf than on the lower. Viewed in transverse section, the outer wall of the epidermis is slightly thickened, and the lumen of the cells is wider on the upper face; the stomata are raised a little above the adjoining epidermis, and have a deep and wide air-chamber. In the lateral parts of the blade, which are much thinner than the median with its broad and thick midrib, the chlorenchyma (*fig. 22*)

shows one layer of typical palisades above a pneumatic tissue of roundish to more or less oblong cells with wide intercellular spaces. However, the stratum of pneumatic tissue which borders on the dorsal epidermis is in some places developed almost as palisades, the cells being more regularly oblong and more compact; as will be shown later, a palisade tissue is very typically represented on both sides of the dorsal keel of the midrib. No crystals were observed in the mesophyll, but long fusiform cystoliths are frequent in the epidermis, especially on the dorsal face.

Collenchyma and stereome seem to be entirely absent from the lateral portion of the blade, and thus the lateral veins are directly imbedded in the chlorenchyma. They are very fine, orbicular in cross-section, and surrounded by a thin-walled, colorless parenchyma sheath.

A more complicated structure is to be found in the median portion of the blade with the strong midrib. Near this part of the blade the leaf is thicker, due to an increase in height of the palisade tissue, while in the midrib a prominent broad and very obtuse keel is to be observed on the dorsal face, and a similar, though much less projecting one, on the ventral. The epidermis is very small-celled in this part of the blade and covers a broad strand of thick-walled collenchyma in about three layers on the dorsal face. There is also collenchyma on the ventral face, and this is extremely thick-walled and represented either by two separate strands near the middle, or by a single one exactly above the center of the midrib. A large, thin-walled colorless tissue occupies the greater portion of the keel, but occurs also above the mestome bundles which compose the midrib. The chlorenchyma is on faces of the midrib interrupted by the collenchyma; it occurs as two strata of high palisades on the ventral face, and as one or two strata of lower palisades (*fig. 23*) in the sides of the keel; thus, as stated above, this tissue is not confined to the ventral part of the blade alone. The pneumatic tissue is also well developed, but only near the dorsal keel. There are three mestome bundles in the midrib; one very broad, in transverse section crescent-shaped with the concave face turned upward, and two very small lateral ones, orbicular in cross-section. A thin-walled endodermis covers the leptome side of these three mestome strands, but not the hadrome.

In the middle there is an arch of thin-walled stereome in two or three layers between the endodermis and the leptome. The leptome has very narrow sieve tubes and companion cells, and the hadrome consists of rather narrow vessels in many short rays. In the two small mestome bundles the mestome is less developed, and there is no stereome. Raphidines abound in the leptome of all three veins, sometimes filling the cells completely.

There are thus in the leaf of *Dianthera* several features indicating the immediate relationship of the genus, illustrated by the structure of the stomata and the presence of raphidines and cystoliths. The distribution of stomata and palisades on both faces of the leaf at least points toward the general structure of an aquatic plant.

THE PETIOLE

There is a short but very distinct petiole, which is approximately hemi-cylindric in outline, the convex face being the dorsal. The internal structure is almost identical with that of the midrib. There are the same tissues of the same development, but distributed in a somewhat different way; for instance, the collenchyma surrounds the colorless parenchyma almost completely, being interrupted only by one narrow group of palisades in the middle of the ventral face, and by two small groups of the same tissue on the sides of the carinate dorsal, and very near its edges. There are three mestome strands in the center, the outline and minor structure of which agree in all respects with the midrib. The petiole has no stereome; cystoliths were found in the epidermis and raphidines in the leptome.

Summary

With the exception of the polystelic axis in *Dianthera*, the structure of the two plants agrees well with that of *Acanthaceae* in general as recorded by SOLEREDER, namely, the type of stomata, the glandular and simple hairs, the cystoliths, the raphidines, the various crystals of calcium oxalate, etc. These characters are some of the most important for distinguishing the family.

Although *Ruellia* and *Dianthera* possess the principal characteristics of the family, the very different environment in which they live has been the immediate cause of several modifications in structure.

In *Ruellia* the structure is that of a land plant as follows: the hairy root with a solid cortex and with many sclerotic cells; the very hairy stem with a closed sheath of stereome inside the endodermis; the very hairy leaves held in a horizontal position and with a strictly bifacial structure in regard to stomata and palisade tissue. In the aquatic *Dianthera*, on the other hand, the roots are glabrous (at least in adult specimens) and the cortex is collapsed; the stem has only small, glandular hairs and the cortex shows intercellular spaces of sometimes enormous width; the narrow leaves are held in a vertical position and are approximately isolateral, so far as concerns the stomata and palisade cells; in addition to the glandular hairs only very short and mostly unicellular hairs cover the margins of the younger leaves.

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EXPLANATION OF PLATES XI AND XII

Ruellia ciliosa

PLATE XI

FIG. 1. Transverse section of root, showing sclerotic cells in the cortical parenchyma. $\times 320$.

FIG. 2. Longitudinal section of a sclerotic cell. $\times 320$.

FIG. 3. Epidermis of lower face of leaf, showing two stomata, a cystolith, and a glandular hair, viewed *en face*. $\times 320$.

FIG. 4. Hair from lower face of leaf. $\times 240$.

FIG. 5. Transverse section of part of midrib of leaf, showing the leptome extending between the hadromatic rays: *end*, endodermis; *l*, leptome; *h*, hadrome. $\times 560$.

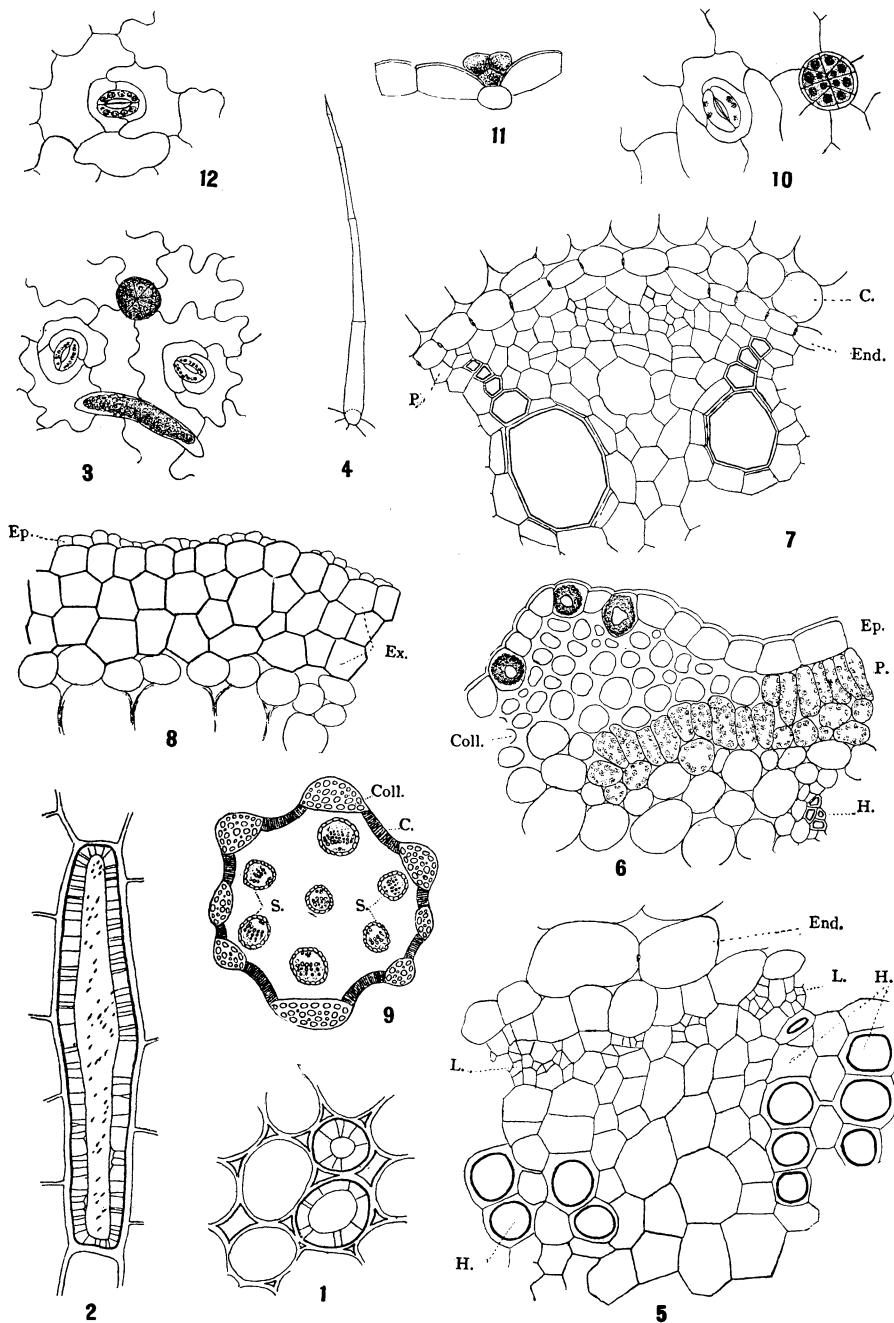
FIG. 6. Transverse section of part of leaf, showing the palisade tissue (*p*) extending above the midrib: *h*, the hadrome of the small lateral mestome bundle; *coll*, collenchyma. $\times 230$.

Dianthera americana

FIG. 7. Transverse section of a secondary root, showing the beginning of growth in thickness: *c*, cortex; *end*, endodermis; *p*, pericambium; between the two rays of vessels and inside the leptome is an arch of cambial tissue and a young, wide, and very thin-walled vessel. $\times 496$.

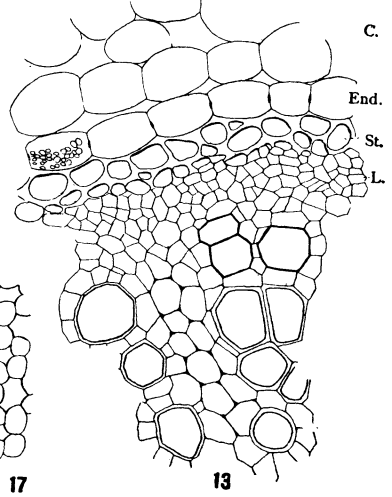
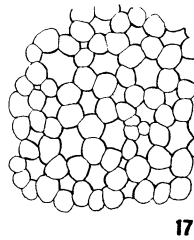
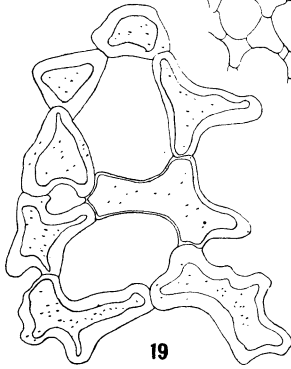
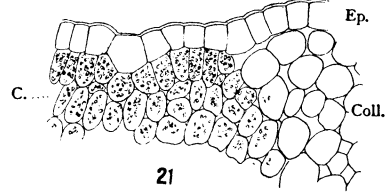
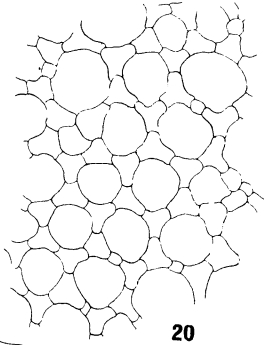
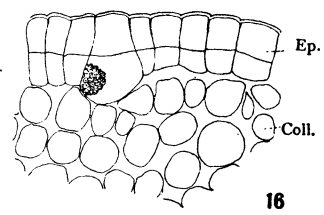
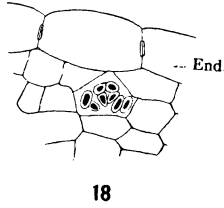
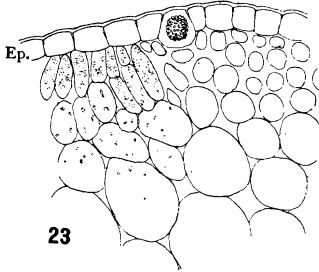
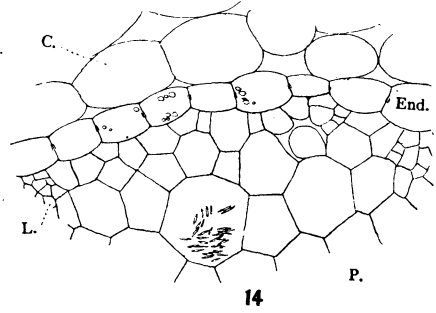
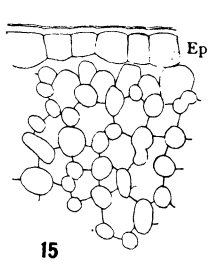
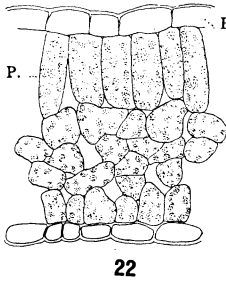
FIG. 8. Transverse section of a secondary root: *ep*, epidermis; *ex*, exodermis of three layers. $\times 320$.

FIG. 9. Transverse section of stem internode, showing eight strands of collenchyma (*coll*) separated by palisades, the peripheral strata of cortex (*c*), and



Auctor ad nat. delin.

HOLM on RUELLIA and DIANTHERA



Auctor ad nat. delin.

seven steles, one in the center, six near the periphery; *s* and *s*, the four steles that fuse together in the node.

FIG. 10. Epidermis of upper face of leaf, showing a glandular hair and a stoma, viewed *en face*. $\times 320$.

FIG. 11. Epidermis and a glandular hair of leaf, transverse section. $\times 320$.

FIG. 12. Epidermis of lower face of leaf with a stoma. $\times 320$.

PLATE XII

FIG. 13. Transverse section of stem internode, showing part of peripheral stele: *c*, cortex; *end*, endodermis; *st*, stereome; *l*, leptome. $\times 400$.

FIG. 14. The innermost face of same stele (*fig. 13*), showing the continuous endodermis, some strands of leptome (*l*), and the large, thin-walled pith (*p*). $\times 400$.

FIG. 15. Transverse section of stem internode, showing the locally, very heavily thickened cell walls of the collenchyma inside epidermis (*ep*). $\times 320$.

FIG. 16. Transverse section of rhizome, showing beginning formation of cork in epidermis (*ep*). $\times 320$.

FIG. 17. Cortex of rhizome, transverse section. $\times 75$.

FIG. 18. Transverse section of rhizome, showing endodermis (*end*) and leptome with raphidines. $\times 560$.

FIG. 19. Transverse section of a node (submersed), showing the very thick-walled, branched cells of cortex. $\times 240$.

FIG. 20. Transverse section of an internode (submersed), showing the open cortex. $\times 75$.

FIG. 21. Transverse section of an aerial internode, showing collenchyma (*coll*) and palisades of cortex (*c*). $\times 320$.

FIG. 22. Transverse section of lateral portion of leaf, showing the ventral epidermis (*ep*) and the palisade tissue (*p*); below is the pneumatic tissue and dorsal epidermis. $\times 240$.

FIG. 23. Transverse section of leaf, showing palisades inside the dorsal epidermis (*ep*), and underneath the midrib. $\times 240$.

FIG. 24. Stoma of upper face of leaf. $\times 320$.